Article

Taxonomy and Phylogeny Reveal Two New Potential Edible Ectomycorrhizal Mushrooms of *Thelephora* from East Asia

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Abstract: The ectomycorrhizal basidiomycetes genus *Thelephora* has been understudied in subtropical ecosystems. Many species of *Thelephora* are important edible and medicinal fungi, with substantial economic value. Two new *Thelephora* species, *T. grandinioides* and *T. wuliangshanensis* spp. nov. are proposed here based on a combination of morphological features and molecular evidence. *Thelephora grandinioides* is characterized by laterally stipitate basidiocarps with a grandinoid hymenial surface, a monomitic hyphal system with clamped generative hyphae, and the presence of tubular and septated cystidia and subglobose to globose basidiospores measuring as 5.3–7.4 × 4–6.5 μm. *Thelephora wuliangshanensis* is characterized by infundibuliform basidiocarps, radially black striate on the pileus, a smooth, umber to coffee hymenial surface, a monomitic hyphal system with thick-walled generative hyphae, and basidiospores that turn greenish grey to buff in 5% KOH. Phylogenetic analyses of rDNA internal transcribed spacer region (ITS) and nuclear large subunit region (nrLSU) showed that the two new *Thelephora* are phylogenetically distinct: *T. grandinioides* is sister to *T. aurantiotincta* and *T. sikkimensis*, while *T. wuliangshanensis* is sister to a clade comprising *T. austrosinensis* and *T. aurantiotincta* with high support as well.

Keywords: corticioid fungi; macro fungi; molecular phylogeny; Thelephoraceae; *Thelephora grandinioides*; *Thelephora wuliangshanensis*; Yunnan Province

1. Introduction

Thelephora Ehrh. ex Willd., the genus type of Thelephoraceae Chevall. is one of the most important taxa in basidiomycetes [1–5]. They are widely distributed worldwide, especially in the northern temperate and tropical regions [1–5]. *Thelephora* is a fairly well-studied ectomycorrhizal basidiomycetes genus with basidiocarps of various shape; the entire genus forms ectomycorrhizal relationships with diverse plants and significant contribution to plant health and ecosystem stability [4,6–12]. As mycorrhiza-formers, *Thelephora* play a very important role in pioneer microhabitats of coniferous forests [13,14]. Acting as white rot fungi, they also can decompose dead wood [14,15].

Some species of *Thelephora* are economically important edible and medicinal mushrooms. *Thelephora ganbajun* M. Zang is one of the most popular edible fungi in China and some East Asian countries [14–21]. *Thelephora* is typified by *T. terrestris Ehrh. ex Willd.* [22],

and the genus is characterized by its diverse forms of basidiomycetes as stereoid, clavarioid, cantharelloid, spathulate, pleuropodally pileate to resupinate; hymenophore smooth to slightly wrinkled and often cyanescent in KOH; pileus surface glabrous to strigose, even or faintly ribbed or papillose; hymenium continuous, usually on inferior side, sometimes amphigenous in some species; hyphal system monomitic with clamped generative hyphae; basidia 4-spored; basidiospores subhyaline to brownish, ornamented, typically muricate, verruculose or echinulate, even or slightly rough-walled in a few species, and inamyloid [1,3,12,22]. As of 2008, fifty species of *Thelephora* have been accepted [23], and some new species have been reported in recent years [4,5,14,24–27]. Index Fungorum [28] shows 871 specific and infraspecific names in *Thelephora*. However, to date, 62 species of *Thelephora* have been accepted [3–5,14,23–27].

Thelephora share similar characteristics with *Tomentella* Pers. ex Pat. especially in the form, size, and type of spore ornamentations [3,29,30]. Based on phylogenetic analyses using rDNA internal transcribed spacer region (ITS) sequences showed that the species of *Thelephora* mixed with *Tomentella*, revealing that both genera are closely related, but it is well-known that the phylogenetic analyses of ITS loci are insufficient to resolve phylogenetic relationships among closely related taxa [4,5,31,32]. Based on ITS and nrLSU analyses, Vizzini et al. [25] showed that *Thelephora* and *Tomentella* species do not separate to two monophyletic groups but they are intermixed and form a well-supported monophyletic clade (*Thelephora*/*Tomentella* clade). Back to traditional method, the most important characteristic for distinguishing *Thelephora* and *Tomentella* is the form of the basidiocarps (resupinate in *Tomentella*; erect, with varied forms, to partially resupinate in *Thelephora*) [24,29,33]. Das et al. [26] proposed that other features such as the hymenophore surface needed to be observed to determine whether it could act as a more informative characteristic than the highly variable stipitate/resupinate configuration of basidiocarps. Phylogenetic analyses of combined ITS and nrLSU dataset in Basidiomycota revealed that *Thelephora* is sister to *Tomentella* nested in Thelephoraceae while the limits between both genera are not yet clear [5,26,34]. While ITS and nrLSU sequences alone cannot resolve phylogenetic relationships in this complex group of species [5,34]. Vizzini et al. [25] mentioned that in the future *Thelephora* and *Tomentella* will be considered as one genus merging *Tomentella* into *Thelephora*.

With this work we intend to identify two *Thelephora* species found in southern China based on morphology and phylogeny, and provide full descriptions, color photographs, a detailed comparison of two new species with closely related taxa and a phylogenetic tree to show the placement of two new species.

2. Materials and Methods

2.1. Specimens Collection and Herbarium Specimen Preparation

Four samples of *Thelephora* were collected in Yunnan (Figure 1A–C) viz. CLZhao 3406 (Holotype) from the Wuliangshan National Nature Reserve, Huangcaoling, Jingdong County, Puer, at latitude 24°18′ N and longitude 101°05′ E, at 2113 m above sea level, 1 October 2017; CLZhao 3408 from the Xieqipo Forest Park, Zhenyuan County, Puer, at latitude 24°18′ N and longitude 101°05′ E, at 1350 m above sea level, 1 October 2017; CLZhao 4107 (Holotype) from the Wuliangshan National Nature Reserve, Huangcaoling, Jingdong County, Puer, at latitude 24°23′ N and longitude 100°45′ E, at 2313 m above sea level, 5 October 2017; CLZhao 21020 from the Wuliangshan National Nature Reserve, Huangcaoling, Jingdong County, Puer, at latitude 23°57′ N and longitude 100°57′ E, 8 October 2020. The fruiting bodies were observed growing on the ground of pine-broadleaved mixed forest. Photographs of the fruiting bodies were taken in the field, macromorphological characteristics were recorded and then the fruiting bodies were collected. The collected fruiting bodies were dried in an electric food dehydrator at 40 °C, then sealed and stored in an envelope bag. They were then transported to mycology laboratory of Southwest Forestry University, Kunming where microscopic morphology and phylogeny were studied.
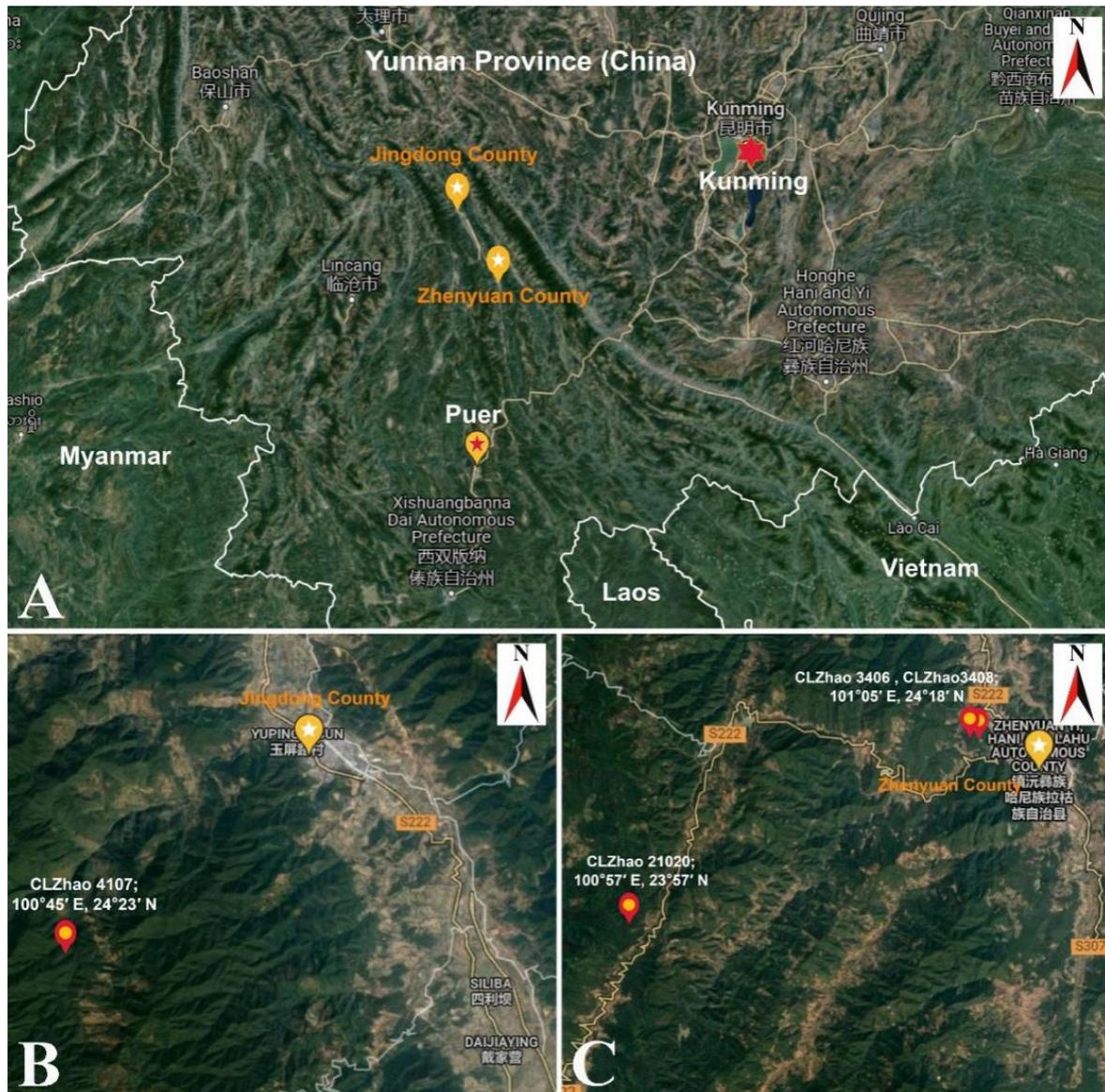
Figure 1. The localities of new *Thelephora* species. (**A**) Jingdong county and Zhenyuan county in Yunnan province. (**B**) The locality of *Thelephora wuliangshanensis* strain (Holotype: CLZhao 4107) in Jingdong county. (**C**) The locality of *T. wuliangshanensis* (CLZhao 21020) and *T. grandinioides* (Holotype: CLZhao 3406; CLZhao 3408) in Zhenyuan county. Source: Map data ©2021 Google.

2.2. Morphology

The specimens studied are deposited at the herbarium of Southwest Forestry University (SWFC), Kunming, Yunnan Province, China. Macromorphological descriptions were based on field notes and photos captured in the field and lab. Color terminology followed Petersen [35]. Micromorphological data were obtained from the dried specimens, and were observed under a light microscope following Dai [36]. The following abbreviations were used: KOH = 5% potassium hydroxide water solution, CB = Cotton Blue, CB– = acyanophilous, IKI = Melzer's reagent, IKI– = both inamyloid and indextrinoid, L = mean spore length (arithmetic average for all spores), W = mean spore width (arithmetic average for all spores), Q = variation in the L/W ratios between the specimens studied, n = a/b (number of spores (a) measured from given number (b) of specimens).

2.3. Molecular Phylogeny

A conventional cetyl trimethylammonium bromide (CTAB) plant genome rapid extraction kit (DN14, Aidlab Biotechnologies Co., Ltd., Beijing, China) was used to obtain genomic DNA from dried specimens, according to the manufacturer's instructions [37]. Amplification reactions were performed in a 30 µL reaction volume composed of 15 µL 2 × FastTaq Premix (a mixture of FastTaq TM DNA Polymerase, buffer, dNTP Mixture, and stabilizer) (Beijing Qingke Biological Technology Co., Ltd., Beijing, China), 1 µL of each of the reverse and forward primers (Beijing Kinco Biotechnology Co., Ltd., Kunming Branch, China), 8.5 µL doble distilled water (ddH2O), and 1–1.2 µL DNA. ITS region was amplified with primer pair ITS5 and ITS4 [38]. The nrLSU was amplified with primer pairs LR0R and LR7 [39]. PCR procedure for ITS followed: initial denaturation at 95 °C for 3 min, followed by 35 cycles at 94 °C for 40 s, 58 °C for 45 s and 72 °C for 1 min, and a final extension of 72 °C for 10 min. For the nrLSU regions, PCR amplification conditions were used as follows: initial denaturation of 1 min at 94 °C, followed by 35 cycles of denaturation at 94 °C for 30 s, 1 min of annealing at 48 °C, 90 s extension at 72 °C, and a final extension of 10 min at 72 °C. PCR products were purified and sequenced at Kunming Tsingke Biological Technology Limited Company, Kunming, Yunnan Province, China. All newly generated sequences were deposited in NCBI GenBank/UNITE (Table 1). Sequences were aligned in MAFFT 7 (https://mafft.cbrc.jp/alignment/server/, accessed on 3 December 2021) using G-INS-i strategy for ITS combined dataset, and manually adjusted in BioEdit [40]. Aligned dataset was deposited in TreeBase (submission ID 28432). *Odontia fibrosa* (Berk. and M.A. Curtis) Kõljalg and *O. ferruginea* Pers. were selected as outgroup for phylogenetic analyses of combined dataset [25,26].

Table 1. Names, vouchers, location, and corresponding GenBank/UNITE accession numbers of taxa used in this study. The newly generated sequences are shown in black bold and T indicates the type.

Taxon Names	Voucher	Location	GenBank/UNITE Accession Number		
			ITS	nrLSU	Reference
Odontia ferruginea	UK18	Estonia	UDB000285	UDB018691	[25]
O. fibrosa	SS38	Sweden	MH310788	UDB018463	[25,26]
Thelephora albomarginata	KHL8457	Sweden	–	UDB018707	[5]
T. americana	UAMH 9578	Chile	AY219838	–	[41]
T. anthocephala	UBC F28410	Canada	KP454019	KP454019	[26]
T. anthocephala	TAA165304	Estonia	AF272927	UDB018693	[27]
T. atra	UK50	Russia	–	UDB018697	UNITE
T. aurantiotincta	115437	–	–	TU115437	UNITE
T. aurantiotincta	520625MF420	China	MZ057686	–	GenBank
T. aurantiotincta	346–518	Japan	AB509809	–	GenBank
T. austrosinensis	GDGM 48867 T	China	MF593265	MF593265	[5]
T. austrosinensis	GDGM 48891	China	MF593266	MF593266	[5]
T. austrosinensis	GDGM 48899	China	MF593267	MF593267	[5]
T. caryophyllea	ELarsson89-09	Sweden	MK602776	MK602776	[42]
T. caryophyllea	TAAM172626	Estonia	–	UDB018694	[5]
T. caryophyllea	TL-6566	Denmark	AJ889980	–	[27]
T. caryophyllea	GO-2010-163	Mexico	KC152242	–	[26]
T. caryophyllea	TAAM172626	Estonia	UDB018694	–	[5]
T. dominicana	JBSD126510 T	Dominican Republic	KX216400	KX216400	[25]
T. ganbajun	Gb151	China	EU696873	–	[9]
T. ganbajun	Gb152	China	EU696874	–	[9]
T. ganbajun	HMAS 276818	China	–	LC164937	GenBank
T. ganbajun	ZRL20151295	China	–	KY418908	[43]
T. grandinioides	**CLZhao 3406 T**	**China**	**MZ400673**	**MZ400675**	**Present study**
T. grandinioides	**CLZhao 3408**	**China**	**MZ400674**	**MZ400676**	**Present study**

Table 1. *Cont.*

| Taxon Names | Voucher | Location | GenBank/UNITE Accession Number | | |
			ITS	nrLSU	Reference
T. iqbalii	MH810 T	Pakistan	JX241471	–	[27]
T. japonica	420526MF0417	China	–	MG712350	GenBank
T. palmata	JMP0085	USA	EU819443	–	[44]
T. palmata	LW 84	–	–	AF291265	[45]
T. palmata	TAA149550	Swedish	AF272919		[44]
T. palmata	Telpa31/38		–	AJ406477	[5]
T. aff. palmata	350–421	Japan	AB509755	–	[27]
T. penicillata	0465	China	MT325773	–	[26]
T. penicillata	LTT8	USA	U83484	–	[46]
T. penicillata	TAAM169453	Estonia	–	UDB018695	[5]
T. pseudoterrestris	TAA159625	Estonia	AF272907	–	[27]
T. pseudoterrestris	UK34	–	UDB000209	–	[25]
T. pseudoversatilis	11H2-1	Mexico	KU530339	–	[26]
T. pseudoversatilis	FCME 26152 T	Mexico	KJ462486	–	[4]
T. pseudoversatilis	FCME 26232	Mexico	JX075890	JX514167	[4]
T. regularis	UBC F33227	Canada	MG953966	–	[26]
T. regularis	JMT17371	USA	U83485	–	[46]
T. aff. regularis	GO-2010-125	Mexico	KC152240	–	[26]
T. aff. regularis	GO-2010-134	Mexico	KC152241	–	[26]
T. sikkimensis	KD 16-003	India	MF684017	–	[26]
T. sikkimensis	KD 16-042	India	MF684018	–	[26]
T. sublilacina	UP161	Sweden	EF493288	–	[27]
T. terrestris	CBS 703.85	Netherlands	–	MH873600	[47]
T. terrestris	Hilszczanska D. 1-IBL	Poland	FJ532478	–	[4]
T. terrestris	P17_M2_772	Poland	KM409440	–	[26]
T. terrestris	UK14	Estonia	–	DB018696	[5]
T. versatilis	MEXU:27094	Mexico	KC595628	–	[4]
T. versatilis	UNAM:FCME26141 T	Mexico	NR154492	–	[4]
T. vialis	Thv1	–	–	AJ406478	[28]
T. wuliangshanensis	**CLZhao 4107 T**	**China**	**MZ400671**	**MZ400677**	**Present study**
T. wuliangshanensis	**CLZhao 21020**	**China**	**MZ400672**	**MZ400678**	**Present study**

Maximum parsimony (MP) analysis was applied to the ITS and nrLSU dataset followed Zhao and Wu [37]. Tree construction procedure was performed in PAUP* version 4.0b10 [48]. All characters were equally weighted and gaps were treated as missing data. Trees were inferred using the heuristic search option with TBR branch swapping and 1000 random sequence additions. Max-trees were set to 5000, branches of zero length were collapsed and all parsimonious trees were saved. Clade robustness was assessed using bootstrap analysis with 1000 replicates [49]. Descriptive tree statistics: tree length (TL), consistency index (CI), retention index (RI), rescaled consistency index (RC), and homoplasy index (HI) were calculated for each Maximum Parsimonious Tree generated. Datamatrix was also analyzed using Maximum Likelihood (ML) approach with RAxML-HPC2 through the Cipres Science Gateway (www.phylo.org, accessed on 3 December 2021) [50]. Branch support for ML analysis was determined by 1000 bootstrap replicates.

MrModeltest 2.3 [51] was used to determine the best-fit evolution model for the data set for Bayesian inference (BI). BI was calculated with MrBayes 3.1.2 [52]. Four Markov chains were run for 2 runs from random starting trees for 160 thousand generations for ITS. The first one-fourth of all generations was discarded as burn-in. The majority rule consensus tree of all remaining trees was calculated. Branches were considered as significantly supported if they received maximum likelihood bootstrap value >60%, maximum parsimony bootstrap value >50%, or Bayesian posterior probabilities >0.90.

2.4. Pairwise Homoplasy Test

The Genealogical concordance phylogenetic species recognition analysis (GCPSR) is a tool used to check significant recombinant events. The data were analyzed using SplitsTree 4 with the pairwise homoplasy Φw, PHI test to determine the recombination level within closely related species [53–55]. One-locus dataset (ITS and nrLSU) with closely related species were used for the analyses. PHI results lower than 0.05 (Φw < 0.05) indicates a significant recombination is present in the dataset. The relationships between closely related taxa were visualized by constructing split graphs from the concatenated datasets, using the LogDet transformation and splits decomposition options.

3. Results

3.1. Molecular Phylogeny

ITS+nrLSU dataset (Figure 2) included 14 sequences representing 9 species, ITS dataset (Figure 3) included 42 sequences representing 23 species, and the nrLSU dataset (Figure 4) consisted of 27 sequences representing 18 species. The ITS+nrLSU dataset had an aligned length of 1887 characters, of which 1514 characters are constant, 123 are variable and parsimony-uninformative, and 250 are parsimony-informative. Maximum parsimony analysis yielded 1 equally parsimonious trees (TL = 616, CI = 0.7403, HI = 0.2597, RI = 0.7217, RC = 0.5343). Best model for the ITS dataset estimated and applied in the Bayesian analysis was GTR + I + G (lset nst = 6, rates = invgamma; prset statefreqpr = dirichlet (1, 1, 1, 1)). Bayesian analysis and ML analysis resulted in a similar topology to MP analysis with an average standard deviation of split frequencies = 0.006269. Estimated base frequencies; A = 0.249341, C = 0.218571, G = 0.275562, T = 0.256526; substitution rates AC = 1.282736, AG = 4.546435, AT = 0.637878, CG = 0.715981, CT = 11.556530, GT = 1.000000; proportion of invariable sites I = 0.502830; distribution shape parameter α = 0.545315. The ITS dataset had an aligned length of 727 characters, of which 355 characters are constant, 87 are variable and parsimony-uninformative, and 285 are parsimony-informative. Maximum parsimony analysis yielded 1 equally parsimonious trees (TL = 1026, CI = 0.5312, HI = 0.4688, RI = 0.7579, RC = 0.4026). Best model for the ITS dataset estimated and applied in the Bayesian analysis was GTR + I + G (lset nst = 6, rates = invgamma; prset statefreqpr = dirichlet (1, 1, 1, 1)). Bayesian analysis and ML analysis resulted in a similar topology to MP analysis with an average standard deviation of split frequencies = 0.009479. Estimated base frequencies; A = 0.219763, C = 0.258778, G = 0.243142, T = 0.278317; substitution rates AC = 1.165884, AG = 5.728342, AT = 0.893563, CG = 0.776446, CT = 8.106172, GT = 1.000000; proportion of invariable sites I = 0.125398; distribution shape parameter α = 0.548666. The nrLSU dataset had an aligned length of 1393 characters, of which 1203 characters are constant, 63 are variable and parsimony-uninformative, and 127 are parsimony-informative. Maximum parsimony analysis yielded 1 equally parsimonious trees (TL = 360, CI = 0.5611, HI = 0.4389, RI = 0.5741, RC = 0.3221). Best model for the nrLSU dataset estimated and applied in the Bayesian analysis was GTR + I + G (lset nst = 6, rates = invgamma; prset statefreqpr = dirichlet (1, 1, 1, 1)). Bayesian analysis and ML analysis resulted in a similar topology to MP analysis with an average standard deviation of split frequencies = 0.009402. Estimated base frequencies; A = 0.263240, C = 0.200643, G = 0.293575, T = 0.242542; substitution rates AC = 1.213148, AG = 7.899379 AT = 0.709533, CG = 0.649904, CT = 18.992697, GT = 1.000000; proportion of invariable sites I = 0.629441; distribution shape parameter α = 0.755239.

The phylogram inferred from ITS+nrLSU, ITS, and nrLSU sequences (Figures 2–4) demonstrated that our specimens formed two isolated branches within *Thelephora* while *T. grandinioides* is sister to *T. aurantiotincta* Corner, and *T. sikkimensis* K. Das, Hembrom and Kuhar, and *T. wuliangshanensis* are sister to a clade comprising *T. austrosinensis* T.H. Li and T. Li and *T. aurantiotincta*.
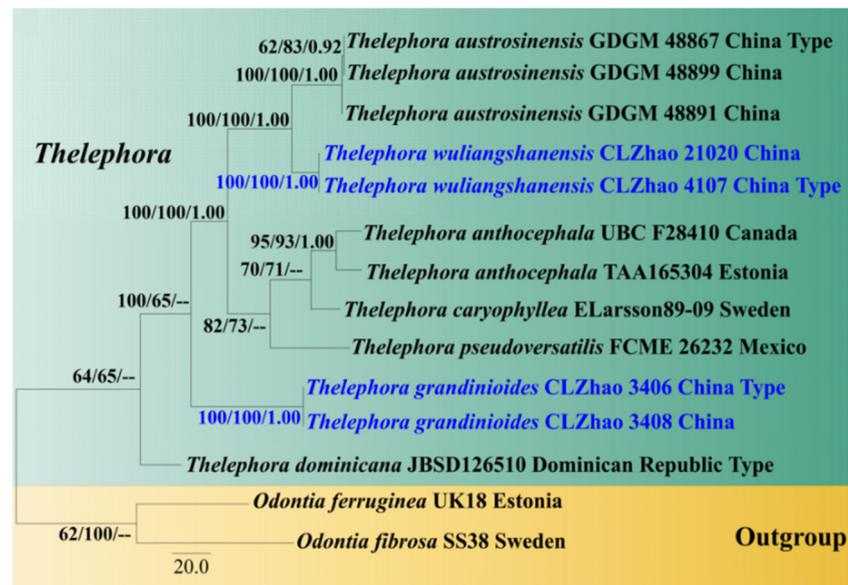
Figure 2. Maximum parsimony strict consensus tree based on the ITS+nrLSU sequences. Bootstrap support values for maximum likelihood (ML) equal to or higher than 60%, Bayesian Probability (PP) equal to or higher than 0.90, and maximum parsimony (MP) bootstrap proportions equal to or higher than 50% are mentioned above the branches (MP/ML/PP). Strains of the newly described species are depicted in blue.
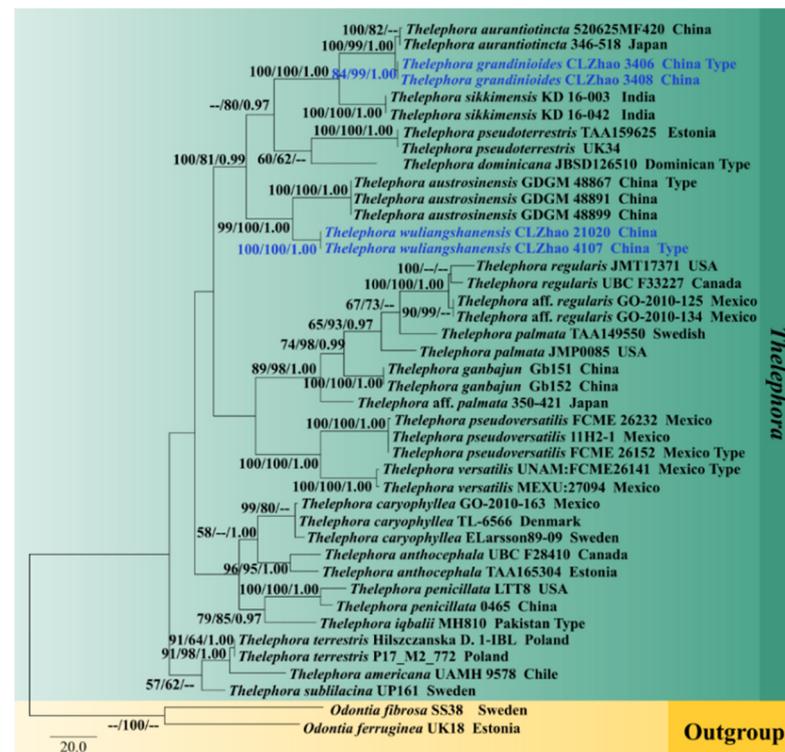

Figure 3. Maximum parsimony consensus tree based on the ITS sequences. Bootstrap support values for maximum likelihood (ML) equal to or higher than 60%, Bayesian Probability (PP) equal to or higher than 0.90, and maximum parsimony (MP) bootstrap proportions equal to or higher than 50% are mentioned above the branches (MP/ML/PP). Strains of the newly described species are depicted in blue.
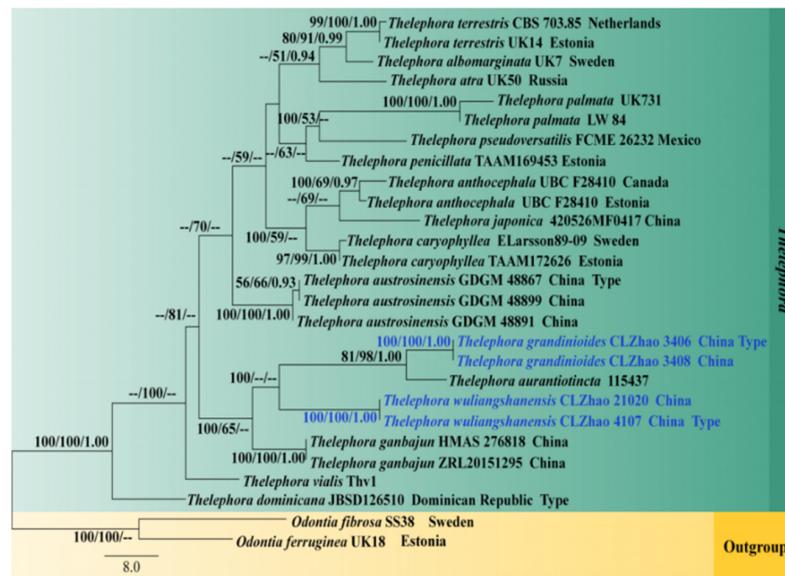
Figure 4. Maximum parsimony strict consensus tree based on the nrLSU sequences. Bootstrap support values for maximum likelihood (ML) equal to or higher than 60%, Bayesian Probability (PP) equal to or higher than 0.90, and maximum parsimony (MP) bootstrap proportions equal to or higher than 50% are mentioned above the branches (MP/ML/PP). Strains of the newly described species are depicted in blue.

Application of PHI test to the ITS and nrLSU tree-locus sequences revealed no recombination level within phylogenetically related species. No significant recombination events were observed between *Thelephora grandinioides* and *T. wuliangshanensis* and phylogenetically closely related species viz. *T. austrosinensis*, *T. ganbajun*, and *T. sikkimensis* (Figures 5 and 6). The test results of ITS sequence dataset show $\Phi w = 0.8271$ ($\Phi w > 0.05$) no recombination is present in the two new species with *T. aurantiotincta*, *T. austrosinensis*, *T. dominicana* Angelini, Losi and Vizzini, *T. ganbajun*, *T. pseudoterrestris* Corner, *T. sikkimensis* and *T. vialis* (Figure 5). The test results of nrLSU sequence dataset show $\Phi w = 0.9964$ ($\Phi w > 0.05$) no recombination is present in the two new species with *T. aurantiotincta*, *T. austrosinensis*, *T. dominicana*, *T. ganbajun*, *T. pseudoterrestris* and *T. vialis* (Figure 6).
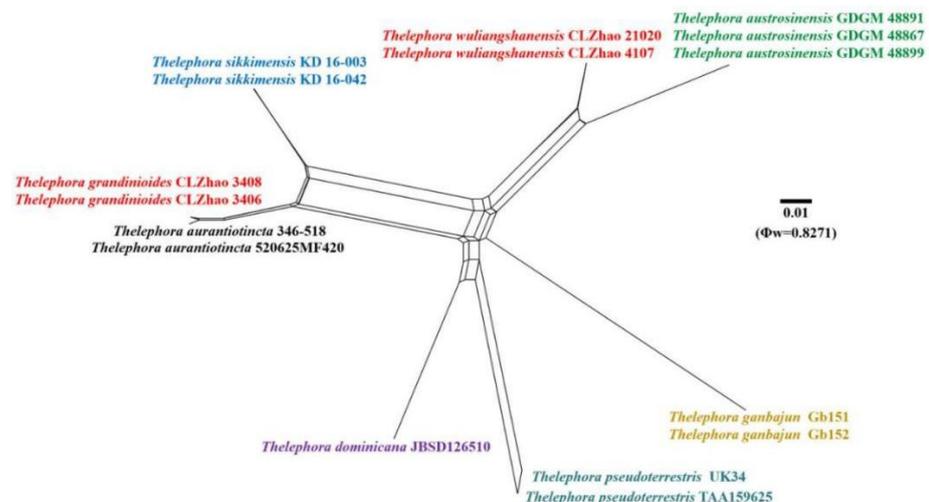

Figure 5. Split graphs showing the results of PHI test for the ITS data of *Thelephora grandinioides* and *T. wuliangshanensis* and closely related taxa using LogDet transformation and splits decomposition. PHI test results $\Phi w \leq 0.05$ indicate that there is significant recombination within the dataset. New taxa are in red while, closly related species to new species are in other colors.
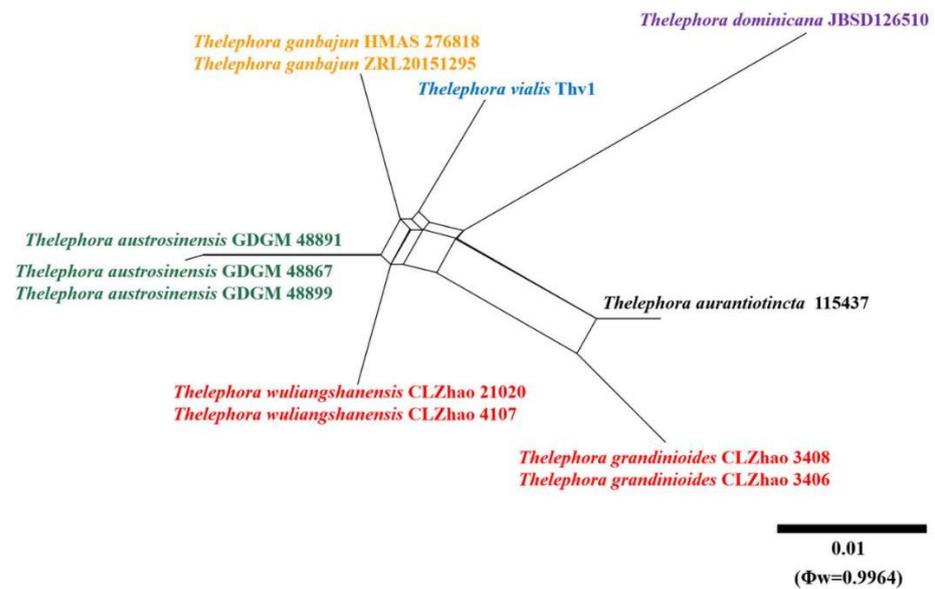
Figure 6. Split graphs showing the results of PHI test for the nrLSU data of *Thelephora grandinioides* and *T. wuliangshanensis* and closely related taxa using LogDet transformation and splits decomposition. PHI test results Φw ≤ 0.05 indicate that there is significant recombination within the dataset. New taxa are in red while, closly related species to new species are in other colors.

3.2. Taxonomy

Thelephora grandinioides C.L. Zhao and X.F. Liu, sp. nov. Figures 7A and 8.

Figure 7. Basidiocarps of *Thelephora grandinioides* (**A**: Holotype CLZhao 3406) and *T. wuliangshanensis* (**B**: Holotype CLZhao 4107). (**A1**) Basidiocarp surface of *T. grandinioides*; (**A2**) Hymenial surface of *T. grandinioides*; (**B1**) Basidiocarp surface of *T. wuliangshanensis*; (**B2**) Hymenial surface of *T. wuliangshanensis*. Bars: (**A1**–**B2**) = 1 cm.
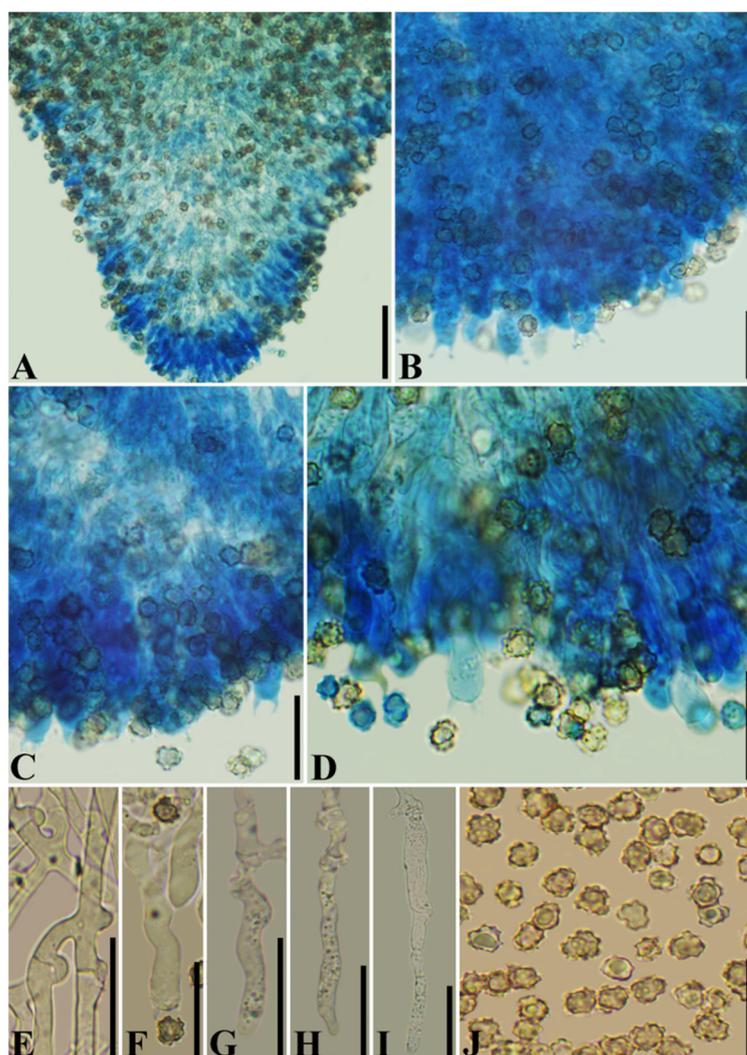
Figure 8. Microscopic structures of *Thelephora grandinioides* (holotype CLZhao 3406). (**A**) A section of hymenium; (**B**) A section of hymenium; (**C**) A section of hymenium; (**D**) A section of hymenium; (**E**) Generative hyphae with clamps; (**F**) Basidia; (**G**) Basidioles: (**H**) Tubular cystidia; (**I**) Septated cystidia; (**J**) Basidiospores. Bars: (**A**) = 50 μm, (**B–I**) = 20 μm.

MycoBank no.: MB840633.

Holotype—China, Yunnan Province, Puer, Zhenyuan County, Xieqipo Park, on the ground of pine-broadleaved mixed forest, 101°05′ E, 24°18′ N, 2113 m a.s.l., 1 October 2017, CLZhao 3406 (SWFC 00003406).

Etymology—*grandinioides* (Lat.): referring to the grandinoid hymenophore of the type specimens.

Basidiocarps—Annual, laterally stipitate, gregarious. Pilei medium-sized, coriaceous, infundibuliform, up to 9 cm long, 7 cm wide, 1.5 mm thick; fawn to isabelline when fresh, greyish brown on drying; proliferous from a central common base, rosulate, usually with several to many laterally confluent spathulate to flabelliform or valves, uplifted; the surface radially striate; margin thin, wavy. Hymenial surface grandinoid, olivaceous buff to clay-buff when fresh, clay-buff to slightly greyish brown on drying. Stipe cylindrical, up to 4 cm long, up to 1.5 cm in diameter. Context fleshy tough to leathery in fresh condition, corky to leathery in dried condition, up to 1 mm thick at the thickest portion of pileus, thinner at margin and thicker toward the base, pinkish buff to buff. Aculei, 6–8 per mm, 0.1–0.2 mm long, greyish brown. Odor mild when fresh, somewhat smelly when dried, or with the beef jerky flavor.

Hyphal system—Monomitic, generative hyphae with clamps, colorless, thick-walled, frequently branched, interwoven, 3–6.5 μm in diameter; IKI–, CB–; tissues turn to greenish grey to buff in KOH.

Hymenium—Cystidia of two types: (1) tubular cystidia, thick-walled, 35–60 × 5–7.5 μm; (2) septated cystidia, numerous, thick-walled, 40–75 × 6–8.5 μm; basidia cylindrical to clavate, slightly constricted in the middle to somewhat sinuous, with 4 sterigmata and a basal clamp, 27–62 × 5–7.5 μm, basidioles dominant, cylindrical, but slightly smaller than basidia.

Basidiospores—Subglobose to globose, nodulose to verrucose or ridged, echinulis 0.5–1 μm, fuscous vinaceous, thick-walled, with guttatae or not, IKI–, CB–, greenish grey to buff in 5% KOH, (5–)5.3–7.4(–7.8) × (3.8–)4–6.5(–7) μm (including ornamentations), L = 6.29 μm, W = 5.31 μm, Q = 1.18–1.21 (n = 60/2).

Additional specimens examined—China, Yunnan Province, Puer, Zhenyuan County, Xieqipo Forest Park, 101°05′ E, 24°18′ N, 1350 m a.s.l., on the ground of pine-broadleaved mixed forest, leg. C.L. Zhao, 1 October 2017, CLZhao 3408 (SWFC 00003408).

Notes—*Thelephora grandinioides* is phylogenetically closely related to *T. aurantiotincta*, *T. dominicana*, *T. sikkimensis*, while *T. wuliangshanensis* is sister to a clade comprising *T. aurantiotincta* and *T. austrosinensis*. The nucleotide differences of phylogenetically similar species to *T. grandinioides* are shown in Table 2. However, morphologically *T. aurantiotincta* differs from *T. grandinioides* by the larger basidiospores (6.5–9 × 5.5–6.5 μm vs. 5.3–7.4 × 4–6.5 μm) and shorter basidia (43–55 × 6.5–8 μm vs. 27–62 × 5–7.5 μm) [3] (Table 4). In addition, the results of BLAST queries in NCBI based on ITS and nrLSU separately are shown in Table 3.

Table 2. The nucleotide differences of phylogenetically similar species to *Thelephora grandinioides* and *T. sikkimensis*.

Species	*Thelephora grandinioides*				*Thelephora wuliangshanensis*			
Specimens	CLZhao 3406		CLZhao 3408		CLZhao 4107		CLZhao 21020	
Gene	ITS (bp)	nrLSU (bp)	ITS (bp)	nrLSU (bp)	ITS (bp)	nrLSU (bp)	ITS (bp)	nrLSU (bp)
T. aurantiotincta 115437	NA	13	NA	13	NA	24	NA	24
T. aurantiotincta 346–518	1	NA	1	NA	42	NA	40	NA
T. aurantiotincta 520625MF420	8	NA	8	NA	78	NA	76	NA
T. austrosinensis GDGM 48891	89	28	89	28	36	17	36	17
T. austrosinensis GDGM 48867	89	29	89	29	37	18	37	18
T. austrosinensis GDGM 48899	87	30	87	30	35	18	35	18
T. dominicana JBSD126510	84	32	83	32	79	26	78	26
T. ganbajun Gb151	98	NA	98	NA	53	NA	52	NA
T. ganbajun Gb152	85	NA	85	NA	78	NA	77	NA
T. ganbajun HMAS 276818	NA	29	NA	29	NA	18	NA	18
T. ganbajun ZRL20151295	NA	27	NA	27	NA	18	NA	18

Table 2. *Cont.*

Species	*Thelephora grandinioides*				*Thelephora wuliangshanensis*			
Specimens	**CLZhao 3406**		**CLZhao 3408**		**CLZhao 4107**		**CLZhao 21020**	
Gene	ITS (bp)	nrLSU (bp)	ITS (bp)	nrLSU (bp)	ITS (bp)	nrLSU (bp)	ITS (bp)	nrLSU (bp)
T. pseudoterrestris UK34	87	NA	87	NA	48	NA	46	NA
T. pseudoterrestris TAA159625	64	NA	64	NA	48	NA	46	NA
T. sikkimensis KD1603	45	NA	45	NA	76	NA	75	NA
T. sikkimensis KD1642	43	NA	43	NA	77	NA	76	NA
T. vialis Thv1	NA	26	NA	26	NA	20	NA	20

Table 3. The top ten species results of Blast search of *Thelephora grandinioides* and *T. sikkimensis* sequences.

Thelephora grandinioides (Holotype CLZhao 3406)						*Thelephora wuliangshanensis* (Holotype CLZhao 4107)					
ITS						**ITS**					
Species	**Max Score**	**Total Score**	**Query Cover**	**E Value**	**Ident**	**Species**	**Max Score**	**Total Score**	**Query Cover**	**E Value**	**Ident**
T. aurantiotincta	1109	1109	94%	0.0	98.87%	*T. ganbajun*	1011	1011	97%	0.0	95.32%
T. sikkimensis	907	907	96%	0.0	92.36%	*T. ganbajun*	1005	1005	97%	0.0	95.16%
T. sikkimensis	872	872	91%	0.0	92.61%	*T. ganbajun*	1000	1000	97%	0.0	95.01%
To. lateritia	806	806	98%	0.0	89.12%	*T. ganbajun*	1000	1000	97%	0.0	95.01%
To. cf. *ramosissima*	802	802	97%	0.0	89.13%	*T. ganbajun*	1000	1000	97%	0.0	95.01%
To. ramosissima	802	802	97%	0.0	89.16%	*T. ganbajun*	1000	1000	97%	0.0	95.01%
To. bryophila	798	798	98%	0.0	88.84%	*T.* cf. *ganbajun*	985	985	95%	0.0	95.22%
To. ramosissima	793	793	96%	0.0	89.15%	*T. ganbajun*	976	976	97%	0.0	94.24%
To. fuscocinerea	793	793	96%	0.0	88.96%	*T. ganbajun*	976	976	97%	0.0	94.25%
T. sp.	987	987	82%	0.0	99.27%	*T.* cf. *ganbajun*	974	974	95%	0.0	94.42%
nrLSU						**nrLSU**					
Species	**Max Score**	**Total Score**	**Query Cover**	**E Value**	**Ident**	**Species**	**Max Score**	**Total Score**	**Query Cover**	**E Value**	**Ident**
To. stuposa	2375	2375	98%	0.0	97.89%	*T. terrestris*	2342	2342	99%	0.0	97.32%
T. terrestris	2342	2342	98%	0.0	97.45%	*T. terrestris*	2331	2331	99%	0.0	97.17%
T. caryophyllea	2340	2340	98%	0.0	97.38%	*T. caryophyllea*	2329	2329	99%	0.0	97.10%
T. terrestris	2331	2331	98%	0.0	97.31%	*To. stuposa*	2320	2320	99%	0.0	97.03%
Pseudotomentella griseopergamacea	2183	2183	98%	0.0	95.35%	*P. griseopergamacea*	2180	2180	99%	0.0	95.15%
P. flavovirens	2165	2165	98%	0.0	95.14%	*P. humicola*	2172	2172	99%	0.0	95.01%
Odontia parvospora	2165	2165	96%	0.0	95.77%	*P. flavovirens*	2170	2170	99%	0.0	95.08%
O. parvospora	2165	2165	96%	0.0	95.77%	*To. pulchella*	2156	2156	99%	0.0	94.94%
P. humicola	2161	2161	98%	0.0	94.99%	*P. tristis*	2128	2128	99%	0.0	94.50%
To. pulchella	2139	2139	98%	0.0	94.84%	*P. tristis*	2122	2122	98%	0.0	94.67%

　　　　Morphologically, *T. grandinioides* is similar to *T. aurantiotincta*, *T. fuscella* Ces. ex Lloyd, *T. gelatinoidea* Lloyd, *T. griseozonata* Cooke, *T. intybacea* Pers., *T. japonica* Yasuda and *T. terrestris* by having a grandinoid or odontoid hymenial surface. However, *T. aurantiotincta* differs from *T. grandinioides* by larger basidiospores (6.5–9 × 5.5–6.5 μm vs. 5.3–7.4 × 4–6.5 μm) and shorter basidia (43–55 × 6.5–8 μm vs. 27–62 × 5–7.5 μm) [3] (Table 4); *T. fuscella*

differs in its shorter basidia (35–45 × 6–7 μm vs. 27–62 × 5–7.5 μm) with 2–4 sterigmata [3] (Table 4); *T. gelatinoidea* differs in having larger basidiospores (7–9.5 × 6–9 μm vs. 5.3–7.4 × 4–6.5 μm) and basidia (45–70 × 8–10 vs. 27–62 × 5–7.5 μm) [3] (Table 4); *T. griseozonata* separates from *T. grandinioides* by having larger basidiospores (8–12 × 5–8 μm vs. 5.3–7.4 × 4–6.5 μm) [3] (Table 4); *T. intybacea* differs from *T. grandinioides* by having larger basidiospores (8–12 × 6–9 μm vs. 5.3–7.4 × 4–6.5 μm) and basidia (45–90 × 9–12 vs. 27–62 × 5–7.5 μm) with 2–4 sterigmata [3] (Table 4); *T. japonica* differs from *T. grandinioides* by having larger basidiospores (7–10 × 6–8 μm vs. 5.3–7.4 × 4–6.5 μm) and smaller basidia (40–55 × 8–10 μm vs. 27–62 × 5–7.5 μm) [3] (Table 4); *T. terrestris* differs from *T. grandinioides* by having larger basidiospores (8–12 × 6–9 μm vs. 5.3–7.4 × 4–6.5 μm) and basidia (40–90 × 8–12 μm vs. 27–62 × 5–7.5 μm) [3] (Table 4).

Table 4. Comparison of Basidiospore, Basidia, Cystidia, Host, Substrate, Location and corresponding references of *Thelelphora* species. The characteristics of newly generated taxa are shown in black bold.

Species	Basidiospore (μm)	Basidia (μm)	Sterigmata	Cystidia (μm)	Host/Substrate	Location	Reference
Thelephora albidobrunnea	8.5–10.5(–11) × 6–8.5	55–80 × 11–13	4		On the ground; *Acer rubrum* L., *Amelanchier canadensis* (L.) Medik., *Amelanchier* sp., *Carpinus caroliniana* Walter	Canada, USA	[3,56–58]
T. alta	7.6–8.5 × 6–7				On the ground	Borneo, Brunei Darussalam, Indonesia, Malaysia	[3,58,59]
T. anthocephala	(7–)8–10(–11) × (5–)6–8.5	40–80 × 7–11	2–4		On the ground in woods; *Fagus* sp., *Queercus* sp.	Austria, China, Denmark, Italy, Netherlands, North Temperate, Norway, Russia, Spain, Slovenia, Sweden, USA, UK	[3,58,60–62]
T. arbuscula	6–7 × 5.5–6				On the ground in forest	India, Mexico, Papua New Guinea; Ukraine	[3,63]
T. atra	9–13 × 8–11	50–100 × 9–12	2–3		On the ground	Spain, Poland	[3,64,65]
T. atrocitrina	8–13 × 6.5–9	45–75 × 8–13	2–4		On the ground in woods (*Abies* sp., *Carpinus* sp., *Fagus* sp., *Quercus* sp.)	Austria, Belgium, Brazilian, Czechoslovakia, France, Germany, Netherlands, Spain	[3,66]
T. aurantiotincta	6.5–9 × 5.5–6.5	43–55 × 6.5–8	4		on the ground in humus in mountain in forest	China, Malaysia	[3,67]
T. austrosinensis	(5.2–)5.7–6.3 (–6.7) × (4.6–)5.0–5.4 (–5.8)	15–24 × 5–7	4		*Castanopsis chinensis* (Spreng.) Hance, *C. fabri* Hance, *C. fissa* (Champ. ex Benth.) Rehder and E.H.Wilson, *C. hystrix* Hook.f. and Thomson ex A.DC., *Lithocarpus polystachyus* (Wall. ex A.DC.) Rehder, *L. uvariifolius* (Hance) Rehder, *Schima superba* Gardner and Champ.	China	[5]
T. bresadolae	5–7				On the ground in woods	Hungary, Czechoslovakia	[3]
T. brunneoviolacea	7.5–11 × 6–8.5		2–4		On the ground in the forest	Congo	[3]
T. caespitulans	7–8 × 5–6				On the ground	Canada, USA	[3]
T. caryophyllea	5–10 × 5–8	47–90 × 8–12	2–4		On sandy ground in coniferous woods; *Betula nigra* L., *Larix occidentalis* Nutt., *Pinus silvestris* L., *Salix sitchensis* Sanson ex Bong.	Canada, China, Georgia, India, Mexico, North temperate, Poland, Russia, Spain, USA	[3,20,60,62,64,67]

Table 4. *Cont.*

Species	Basidiospore (μm)	Basidia (μm)	Sterigmata	Cystidia (μm)	Host/Substrate	Location	Reference
T. cerberea	8–11 × 6–8.3		2–4		On the ground in dry forest	Congo	[3]
T. cervicornis	7–8.5 × 6.5–7.5				On the ground	Bahamas, Mexico, USA	[3,68]
T. cervina	6–7.5 × 5–6				On the ground	China	[3]
T. congesta	8.5–11 × 5.5–8.3	30–40 × 7–8	4		On the ground	Australia	[3]
T. crassitexta	9–11 × 6–9	65–100 × 10–12	2–4		On the wood	Borneo	[3]
T. cuticularis	7.5–12.5 × 6–9				On mossy bark at the base of trees and on fallen twigs; *Juniperus virginiana* L.	UK, USA	[3,56,57]
T. cylindrica	8–11 × 6.5–9	80–110 × 11–14	4		On the ground in the forest	Japen, Java, Sumatra,	[3]
T. dactylites	6.5–8 × 5–7		4		On the ground	China	[3]
T. dentosa	7–9 × 6.5–8	18–46 × 8–13	4	19–36 × 4.5–7.5	On dead twigs and leaves and encrusting parts pf living plants	Brazilian, Cuba; Haiti, Indian, Jamaica, Mexico	[3,66,69]
dominicana	8–9.6 × 7.2–8.8	(30–)50–60 × 10–12	4		on deciduous forest litter; On the ground of deciduous forest; *Coccoloba* spp.; *Gymnopodium floribundum* Rolfe	Dominican Republic, Mexico	[14,25]
T. erebia	9–12 × 7–10	45–60 × 10–12	2		On the ground in the forest	Malaysia	[3]
T. fragilis	6–7 × 4–5	14–28 × 5–7	2–4		On the ground in the forest	Malaysia, Philippines	[3]
T. fucoides	7–9 × 6–8				On the ground in the forest	India, Malaysia, Pakistan, USA	[3]
T. fuscella	6–8 × 4.5–6	35–45 × 6–7	2–4		On the ground; Symbiotic with plants	China, Europe, India, Japan, Malaysia, Nepal, North America, Singapore	[3,11,70]
T. ganbajun	7–12 × 6–8	25–35 × 9–12	4	52–80 × 7–14	In the root of *Pinus yunnanensis* Fr. and *Pinus kesiya* var. *langbianensis*	China	[5,18,21]
T. gelatinoidea	7–9.5 × 6–9	45–70 × 8–10	4		On the ground in the forest	China, India, Malaysia	[3]
gelidioides	6–8 × 4.5–6				On the ground in the forest	Singapore	[3]
T. grandinioides	**(5–)5.3–7.4(–7.8) × (3.8–)4–6.5(–7)**	**27–62 × 5–7.5**	**4**	**35–60 × 5–7.5**	**On the ground of pine-broadleaved mixed forest**	**China**	**Present study**
T. griseozonata	8–12 × 5–8				on sandy ground in pine wooods (*Pinus* sp.)	Germany, Puerto Rico, New Zealand, USA, Virgin Islands	[3,56]
T. intybacea	8–12 × 6–9	45–90 × 9–12	2–4		In pine woods; *Cedrus deodara* (Lamb.) G.Don, *Pinus canariensis* C.Sm.	European, New Zealand, North America, Southern Africa, Uruguay, USA	[3,56]
T. investiens	8.5–10 × 7–9.5		4		On the ground in forest	Malaysia	[3]
T. japonica	(6–)7–10 × (5.5–)6–8	40–55 × 8–10	2–4		On the ground, often encrusting small living plants; Ectomycorrhizal, humicolous, gregarious in mixed forest of *Populus nigra* L. and *Salix alba* L.	China, India, Japan, Malaysia	[3,12]
T. lutosa	5–6 × 3.5–4				On the ground in roads and in woods	USA	[3,56]
T. luzonensis	5–6.5 × 4.7–5.7		2–3			China; Philippines, USA	[3]

Table 4. *Cont.*

Species	Basidiospore (μm)	Basidia (μm)	Sterigmata	Cystidia (μm)	Host/Substrate	Location	Reference
T. magnifica	9–12 × 7–9	60–75 × 8–10	2–3–4		On ground in hill dipterocarp forest	Brunei, Malaysia	[3,71]
T. magnispora	11–12 × 9–11	50–70 × 10–11	4		On mossy ground	Indian, Jamaica, USA	[3,72]
T. mollissima	8.5–10.7 × 6–7.7				In woods	European, China	[3,60]
T. multipartita	6–8.5(–9) × 4.7–7				On the ground in frondose woods; *Quercus* sp.	Canada, China, Japan, USA, Venezuela	[3,56,60]
T. nigrescens	6–9 × 5–8	30–50 × 7–10	4, rarely 2–4		On the ground	Brunei Darussalam, China, Indonesia, Japan, Philippines	[3,58]
T. palmata	8–12 × 7–9	70–100 × 9–12	2–4		On the ground in coniferous woods; *Pinus* sp.; *Quercus humboldtii* Bonpl.	China, Colombia, France, North temperate, Russia, Sweden, UK, USA	[3,56]
T. paraguayensis	6.5–8.5 × 4.5–7		4		On the ground in woods	Brazil; Columbia; Paraguay	[3,58]
T. pendens	8–10 × 7–8	40–50 × 10–12	4		Rotten wood in the forest	Malaysia	[3]
T. penicillata	7–10 × 5–8	30–75 × 7–11			On the ground and crusted leaves, branches, grass; *Quercus coccifera* L.	Canada, China, Galapagos Islands, India, Russia, UK	[3,60]
T. phyllophoroides	5–7.5 × 4.5–5.5				On the ground	Japan	[3]
T. pseudoterrestris	9–11.5 × 7–9	50–60 × 12–14			On the ground in the forest, leaves	Malaysia	[3]
T. pseudoversatilis	(6–)7–8(–8.5) × (5–)5.5–6(–7)	47–55 × 9–12	4		Sub-perennial tropical forest	Mexico	[4]
T. ramarioides	7–12.5 × 5–8.5	46–70 × 5–12	2–4, rarely 6–8	50–150 × 5–12	On the ground under *Casuarina equisetifolia* L.	Australia, Borneo, Java, Malaysia	[3]
T. regularis	6–8 × 4.5–6.5	35.2–102.4 × 6.4–9.6	4		In moss in wet places and in humus; Ectomycorrhizal, humicolous, scattered under *Salix excelsa* J.F.Gmel., *S. alba* L. and *Populus nigra* L.	Canada, India, USA	[3,12,56]
T. scissilis	6–8.5 × 5–7		4		On the ground in oak forest	Borneo, India, USA	[3]
T. sikkimensis	6–(7.3)–8.8 × 5–(6.26)–7	35–65 × 7–9	4	30–50 × 3–10	On the ground of *Castanopsis hystrix*	India	[26]
T. spiculosa	8–12 × 7.5–9	60–70 × 9–12			Encrusting coniferous needles of *Pinus* sp.	France, Japan, Sweden, UK	[3,57]
T. tenuis	7–8 × 6–7				On sandy ground	China, Russia	[3]
T. terrestris	8–12 × 6–9	40–90 × 8–12	2–4		On the ground in coniferous, on roots, syumps and seedlings; *Picea abies* L.; *Picea sitchensis* (Bong.) Carr.	Australia, Bavaria, Brazil, China, Europe, Germany, Indian, Jamaica, Japan, Mexico, New Zealand, North America, South Africa, Spain, UK, Uruguay, USA	[3,21,60,64,67,68,72]
T. versatilis	6–7(8.5) × (4) 5–6(6.5)	30–86 × (7)8–11	4		Deciduous and sub-perennial tropical forest	Mexico	[4]
T. vialis	4.5–7(–8) × 4.5–6(–6.5)	26.4–64.0 × 5.6–10.4			On the ground in frondose woods; Ectomycorrhizal, humicolous, scattered to gregarious in the mixed forest of *Populus nigra* L., *Salix alba* L. and *Hippophae rhamnoides* L.	China, India, Japan, North America, USA	[3,12,56,60,73]

Table 4. *Cont.*

Species	Basidiospore (μm)	Basidia (μm)	Sterigmata	Cystidia (μm)	Host/Substrate	Location	Reference
T. wakefieldiae	40–65 × 7.5–12	40–65 × 7.5–12	4		Colonizes all kinds of wood debris	Denmark, Estonia, France, Germany, North temperate, Norway, Spain, Russia, Sweden, UK, USA	[14]
T. wuliangshanensis	(5–)5.2–8.7(–9.3) × (3.7–)4.5–7.2 (–7.6)	30–60 × 5–9.5	4	28–55 × 3–7.5	**On the ground of pine-broadleaved mixed forest**	**China**	**Present study**
T. zeylanica	8–12 × 4–8.5				On the ground	Ceylon	[3]

Thelephora grandinioides morphologically resembles *T. ganbajun* and *T. ramarioides* D.A. Reid due to the presence of cystidia. However, *T. ganbajun* differs from *T. grandinioides* by its larger basidiospores (7–12 × 6–8 μm vs. 5.3–7.4 × 4–6.5 μm), shorter basidia (25–35 × 9–12 μm vs. 27–62 × 5–7.5 μm), and larger cystidia (52–80 × 7–14 μm vs. 35–60 × 5–7.5 μm) [17] (Table 4); *T. ramarioides* differs from *T. grandinioides* by its larger basidiospores (7–12.5 × 5–8.5 μm vs. 5.3–7.4 × 4–6.5 μm) and smaller basidia (46–70 × 5–12 μm vs. 27–62 × 5–7.5 μm) [3] (Table 4).

Thelephora wuliangshanensis C.L. Zhao and X.F. Liu, sp. nov. Figures 7B and 9.

MycoBank no.: MB840634.

Holotype—China, Yunnan Province, Puer, Jingdong County, Huangcaoling, Wuliangshan National Nature Reserve, 100°45′ E, 24°23′ N, 2313 m a.s.l., on the ground of pine-broadleaved mixed forest, leg. C.L. Zhao, 5 October 2017, CLZhao 4107 (SWFC 00004107).

Etymology—*wuliangshanensis* (Lat.): referring to the provenance (Wuliangshan) of the type specimens.

Basidiocarps—Annual, laterally stipitate, gregarious. Pilei small to medium-sized, coriaceous, infundibuliform, up to 5.5 cm long, 4.5 cm wide, 1 mm thick; buff to salmon when fresh, pinkish buff to cinnamon-buff on drying; proliferous from a central common base, usually with several to many laterally confluent spathulate to flabelliform, uplifted; the surface radially black striate; margin thin, serrulate. Hymenial surface smooth, umber to coffee when fresh, coffee on drying. Stipe cylindrical, up to 2 cm long, up to 5 mm in diameter. Context fleshy tough in fresh condition, leathery in dried condition, up to 0.7 mm thick at the thickest portion of pileus, thinner at margin and thicker towards the base, pinkish buff. Odor mild when fresh, somewhat with the beef jerky flavor.

Hyphal system—Monomitic, generative hyphae with clamps, colorless, thick-walled, frequently branched, interwoven, 2.5–6 μm in diameter; IKI–, CB–; tissues turn to greenish grey in KOH.

Hymenium—Cystidia tubular, thick-walled, 28–55 × 3–7.5 μm; basidia barrel-shaped to slightly clavate, with 4 sterigmata and a basal clamp, 30–60 × 5–9.5 μm, basidioles dominant, clavate, but slightly smaller than basidia.

Basidiospores—Subglobose to globose, nodulose to verrucose, echinulis 0.5–1 μm, umber purple, thick-walled, with guttatae or not, IKI–, CB–, greenish grey to buff in 5% KOH, (5–)5.2–8.7(–9.3) × (3.7–)4.5–7.2(–7.6) μm (including ornamentations), L = 7 μm, W = 5.66 μm, Q = 1.23–1.25 (n = 60/2).

Additional specimens examined—China, Yunnan Province, Puer, Zhenyuan County, Huangcaoling, Wuliangshan National Nature Reserve, 100°57′ E, 23°57′ N, on the ground of pine-broadleaved mixed forest, 8 October 2020 CLZhao 21020 (SWFC 00021020).

Notes—*Thelephora wuliangshanensis* is sister to a clade comprising *T. aurantiotincta* and *T. austrosinensis* in phylogeny; and the nucleotide differences of phylogenetically similar species to *T. sikkimensis* are shown in Table 2. *Thelephora sikkimensis* differs from *T. grandinioides* by its shorter cystidia (30–50 μm vs. 35–60 μm) and hairy basidiocarp surface [26] (Table 4). *Thelephora aurantiotincta* separates from *T. wuliangshanensis* by smaller

basidia (43–55 × 6.5–8 μm vs. 30–60 × 5–9.5 μm) [3] (Table 4); while *T. austrosinensis* differs from *T. wuliangshanensis* by its smaller basidiospores (5.7–6.3 × 5.0–5.4 μm vs. 5.2–8.7 × 4.5–7.2 μm) and basidia (15–24 × 5–7 μm vs. 30–60 × 5–9.5 μm) [27] (Table 4). In addition, the results of BLAST queries in NCBI based on ITS and nrLSU separately are shown in Table 3.
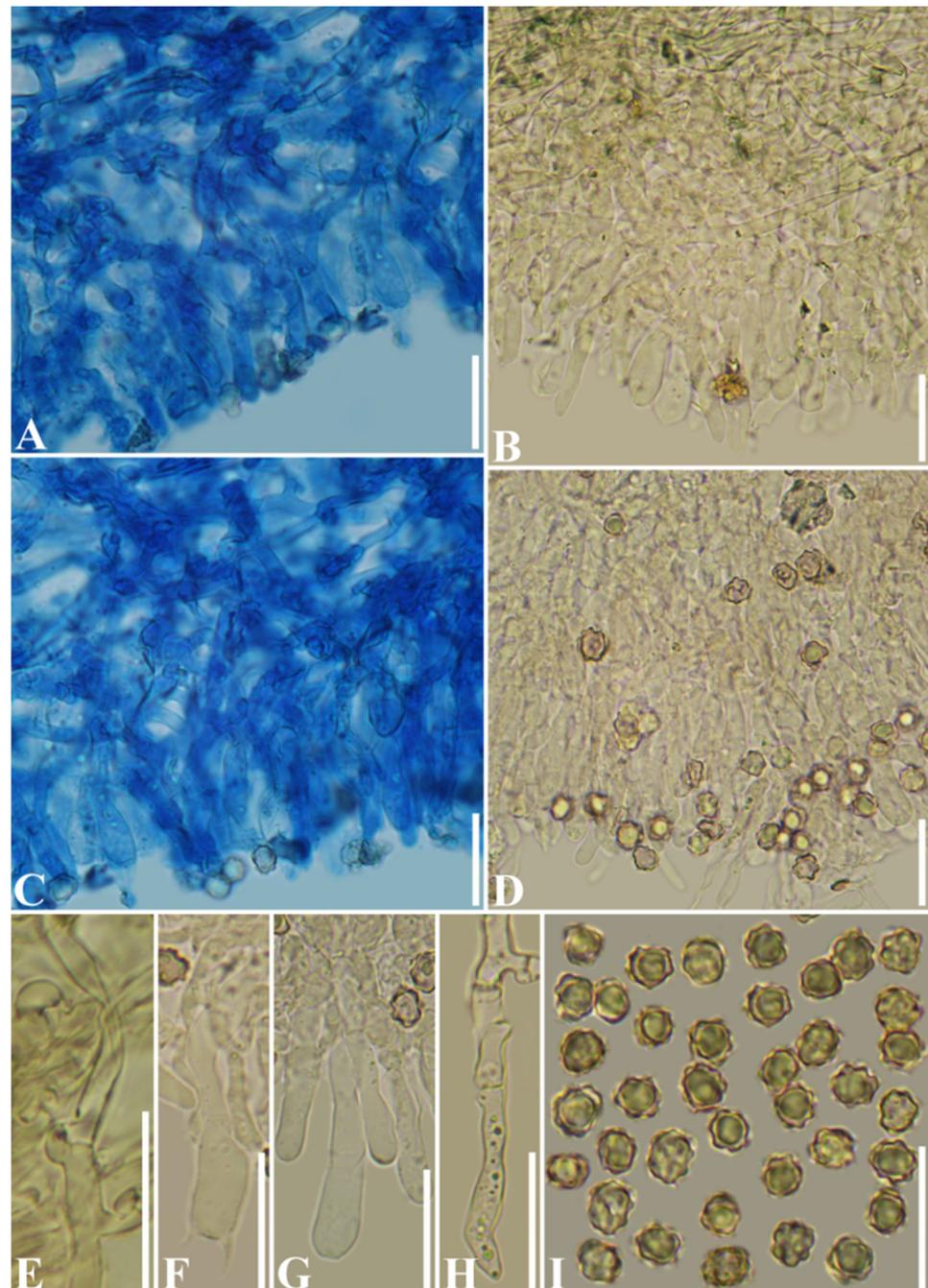

Figure 9. Microscopic structures of *Thelephora wuliangshanensis* (Holotype CLZhao 4107). (**A**) A section of hymenium; (**B**) A section of hymenium; (**C**) A section of hymenium; (**D**) A section of hymenium; (**E**) Generative hyphae with clamps; (**F**) Basidia; (**G**) Basidioles: (**H**) Cystidia; (**I**) Basidiospores. Bars: (**A**–**I**) = 20 μm.

4. Discussion

In the present study, two new species, *Thelephora grandinioides* and *T. wuliangshanensis* are described based on phylogenetic analyses and morphological characteristics. In addi-

tion, the PHI test (Figures 5 and 6) was carried out to confirm there is no recombination present in the two new species compared with closely related taxa.

Thelephora, a genus with diverse basidiocarp forms, are widely distributed worldwide [3,26,28]. Basidia form is an important characteristic of intraspecific identification in *Thelephora*, and most species of *Thelephora* have 4-spored basidia, there are 2-spored (*T. erebia*), 2–3-spored (*T. atra* and *T. luzonensis*), 2–4-spored (*T. anthocephala*, *T. atrocitrina*, *T. brunneoviolacea*, *T. caryophyllea*, *T. cerberea*, *T. crassitexta*, *T. fragilis*, *T. fuscella*, *T. intybacea*, *T. japonica*, *T. magnifica*, *T. nigrescens*, *T. palmata*, and *T. terrestris*) and sometimes there are 6–8-spored (*T. ramarioides*) [3–5,21] (Table 4).

Thelephora is closely related to *Tomentella* both in morphology and phylogeny [5,10,14,25,29,74]. Molecular phylogenetic analyses of previous studies showed that the taxa of *Thelephora* and *Tomentella* are non-monophyletic groups, and they are intermixed in molecular phylogeny [4,5,25,29,31,33]. Traditionally, the form of basidiocarps is the most important characteristic in distinguishing *Thelephora* and *Tomentella*, which are resupinate in *Tomentella*, but erect, with varied forms, to partially resupinate in *Thelephora* [3,14,24,25,29,34,74]. The variations in basidiocarp form may also complicate the characteristics of taxa [75,76], and the results of the morphological investigations and molecular phylogenetic analyses suggested that basidiocarp reduction happened several times independently across the evolution of thelephoroid fungi [14,25]. Taxa with reduced basidiocarps should be taken into account in the diagnoses of genera for which the initial descriptions did not cover a real spectrum of polymorphism and trends of morphological rationalization in connection with colonization of specific habitats [14,25,76]. According to molecular data, only one genus may be recognized, and *Tomentella* will be merged into *Thelephora* [25].

In the habitat and distribution, thelephoroid fungi have a circumglobal distribution, ranging from polar deserts [9] to tropical forests [3], but their peak diversity is observed within the boreal zone of the planet [14,33]. Most of the species in this group have ectomycorrhizal associations [77,78], but it is also capable of destroying wood debris as white rot producers [14,15]. The species of *Thelephora* are a widely distributed group found on six continents except Antarctica [3,5,14,17,26], mainly distributed across Europe in Austria, Bavaria, Belgium, Denmark, Estonia, France, Georgia, Germany, Italy, Netherlands, Norway, Poland, Russia, Slovenia, Spain, Sweden, UK and Ukraine [3,5,28,58,59,62,65,66,76]; additionally, the most-common substrata are hardwood and conifer [3,5]. It is also distributed in Asia (Borneo, China, Japan, India, Malaysia, Nepal, Pakistan, Philippines, Sri Lanka, and Singapore) [3,5,56–58,60,67,70,71], North America (Bahamas, Canada, Cuba, Dominican Republic, Haiti, Jamaica, Mexico, and USA) [3,5,14,25,56–58,62,63,69], South America (Uruguay) [3], Oceania (Australia and Papua New Guinea) [3], and Africa (Congo and Southern Africa) [3,5,56] seen in Table 4. Twenty one species of *Thelephora* have been reported from China (including our two new species), in which *T. ganbajun* and *T. vialis* Schwein. are the two most commonly reported taxa, and the former is one of the most popular edible fungi in Southwest China [5,17–20,60,61,67–79]. The diversity of *Thelephora* in China is still not well-known, especially in the subtropical and tropical regions and many recently described taxa of thelephoroid fungi are from these areas [5,67]. *Thelephora grandinioides* and *T. wuliangshanensis* are also from subtropics. According to our statistics, twenty-one *Thelephora* species have been recorded in China (Table 4), in which 7 are edible and 4 are medicinal (*T. aurantiotincta*, *T. ganbajun*, *T. terrestris*, and *T. vialis*) with anticancer properties, treat leukemia, boost immunity, and are an anti-allergic agent (Table 5). Fleshy to coriaceous basidiocarps, a mild odor, and beef jerky flavor are characteristics of *T. grandinioides*. Several *Thelephora* species are known as edible or medicinal mushrooms, while our new species are potential edibles thus, secondary metabolite analyses of the two new species should be carried out in the future.

Table 5. Edible and medicinal species of *Thelelphora*.

Species	Edible Value	Medicinal Value	Medicinal Efficacy	Reference
Thelephora anthocephala		P	Anticancer	[80]
T. aurantiotincta	Y	Y	Anticancer	[73,80–85]
T. austrosinensis	Y			[5]
T. caespitulans		P	Anticancer	[82]
T. caryophyllea		P	Anticancer	[82]
T. fuscella	Y			[81]
T. ganbajun	Y	Y	Treat leukemia, anticancer and boost immunity	[5,83,85–88]
T. intybacea		P	Anticancer	[80]
T. japonica	Y	P	Anti-microbial activities	[20,81,88,89]
T. palmata	Y	P	Anticancer	[81,82]
T. penicillata		P	Anticancer	[80]
T. regularis		P	Anticancer	[80]
T. scissilis		P	Anticancer	[80]
T. sikkimensis	P			[26]
T. terrestris		Y	Anticancer	[90]
T. vialis	Y	Y	Anticancer and anti-allergic agent	[73,91,92]

"Y" means have edible or medicinal value; "P" means have edible or medicinal potential.

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